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Spawning season and temperature relationships for sardine (*Sardina pilchardus*) in the eastern North Atlantic

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Spawning temperature preferences for sardine (*Sardina pilchardus*) in the eastern North Atlantic were determined from egg survey data. These were compared with climatological temperature cycles (1986–2002) derived from satellite observations, by geographical region, to predict spawning seasons. Optimum spawning temperatures were determined as 14.0–15.0°C from the English Channel to Portugal and 16.0–18.0°C for all north-west African regions. Spawning seasons were closely related to the general latitudinal trend of the annual temperature cycle, with modification by upwelling in the western Iberian and north-west African regions. Some differences between temperature-based spawning season predictions and field observations were related to variations in seasonal plankton production. Correlations in the annual time-series of favourable spawning temperatures suggested relatively strong linkages between the southern areas from Portugal to Senegal. There was no consistent relationship between annual variations in extent of temperature-predicted spawning seasons and observed field abundance of eggs.

INTRODUCTION

Temperature influences many aspects of spawning in marine fish, as well as being related to subsequent survival of eggs and larvae (Heath, 1992). Sardine (*Sardina pilchardus* Walbaum, 1792) in the eastern North Atlantic spawn over an extensive geographical range, from north-west Africa to the British Isles, and experience a variety of oceanographic conditions, from temperate shelf seas to sub-tropical upwelling, at temperatures from <10°C to >22°C. Furthermore, small pelagic species, such as sardine, are particularly sensitive to temperature change, which is reflected in varying historical distributions (e.g. Alheit & Hagen, 1997). It was in this context that the present study was initiated, the aims being: (1) to determine the regional temperature preferences for sardine spawning; (2) to relate spawning times to regional temperature cycles; and (3) to examine the potential influence of inter-annual temperature variation on spawning. This work forms part of a larger study (SARDYN) on population structure of sardine in the eastern North Atlantic.

MATERIALS AND METHODS

*Sea-surface temperature (SST) and chlorophyll-*a

The SST (1986–2002) from the National Oceanic and Atmospheric Administration/National Aeronautics and Space Administration 5-channel AVHRR (advanced very high resolution radiometer) Ocean Pathfinder dataset (Vazquez et al., 1995) and chlorophyll-*a* (1997–2002) derived from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) using the OC4 algorithm (O'Reilly et al., 1998), were used to construct monthly climatologies. Data were extracted for 585 adjacent pixels along a 5400 km mid-shelf line between the coast and the 200 m isobath from 15 to 50°N (Figure 1); data along this line were taken as representative of environmental conditions for the predominantly on-shelf spawning distribution of sardine. The line was sub-divided into eight bio-physical 'areas' based on a combination of criteria, including temperature and oceanographic regime, sardine spawning biology, egg survey regions and fisheries divisions (Figure 1).

Spawning temperatures

Characterization of sardine spawning temperatures was based on the data sources listed in Table 1. These include results from vertical and oblique net tows for annual spawning stock egg surveys off Portugal, northern Spain and in eastern Biscay. For the English Channel area, the data are monthly means of routine weekly egg sampling at the western English Channel time-series Station L5 (Southward et al., 2005). For the north-west African areas there were insufficient data for objective calculation of parameters; hence a subjective estimate was used, based on available published information (see Appendix).

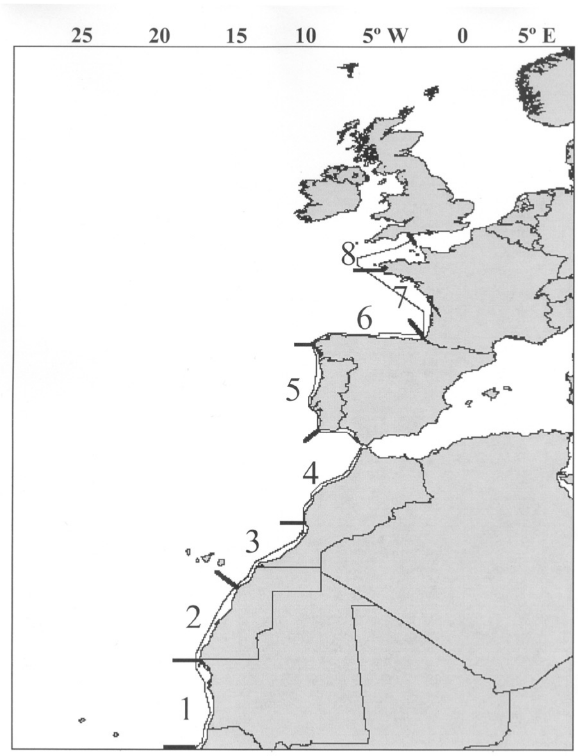

Figure 1. Mid-shelf line along which SST and chlorophyll-*a* data were extracted and the eight area divisions.

RESULTS

Spawning temperatures

Based on temperature weighted by egg abundance at each sampling station, the calculated mean, optimum (defined as the temperature range including 50% of egg abundance) and overall (defined as the temperature range including 95% of egg abundance) spawning temperatures by area are listed in Table 2 and plotted in Figure 2. The following qualifications on potential bias are noted:

- Results for the English Channel are based on data from a single station, whereas for eastern Biscay, northern Spain and Portugal, the data are from egg surveys with more representative wider geographical coverage.
- Year-round time-series sampling, as for the English Channel data, will tend to give a wider overall spawning temperature range than values in the other areas, which are derived from egg surveys confined to a few months of peak spawning.
- The eastern Biscay sampling is targeted on anchovy (*Engraulis encrasicolus*), which spawns later and in warmer conditions than sardine; hence, with a potential positive bias in the derived temperature parameter values for sardine in that area; additionally, these data were available for a short series of years only.
- The values for the four north-west African regions are estimates based on limited sampling.

Relationship of spawning to regional temperature and production cycles

Considering the above qualifications on bias and representation of the different data sets, a generalized set of values for spawning temperatures were concluded for areas 1–4 (north-west Africa) and areas 5–8 (Portugal to the English Channel), respectively, as: (a) optimum ranges of 16.0–18.0°C and 14.0–15.0°C; and (b) overall ranges of 15.5–20.0°C and 12.5–17.0°C. These ranges are plotted in Figure 3 with the corresponding climatological temperature and chlorophyll-*a* cycles, in order to identify the timing of potential spawning seasons (Figure 4) and their relationship with production levels.

The series of temperature cycles (Figure 3A) show the general latitudinal trend of increasing temperature towards the equator, with variations by area due to modification by regional oceanographic conditions, principally the timing and extent of upwelling (see Wooster et al., 1976 and Roy et al., 1989). Considering the three most northerly areas, the cooler conditions in the English Channel are evident, compared with the two similar annual cycles, but with increased summer warming ($\Delta T > 7°C$), in eastern Biscay and off northern Spain; this difference is due to the less extensive seasonal stratification in the English Channel. Relatively low seasonal warming ($\Delta T \sim 4°C$) is seen off Portugal and southern Morocco; both these areas experience moderate summer upwelling, which reduces peak summer temperatures. In the

Table 1. *Data sources for spawning temperature parameters. Survey dates are coded by month (m) and year (y) in the format mmyy.*

Area 1—Senegal and Mauritania	From north-west African spawning references (see Appendix)
Area 2—Western Sahara	As above
Area 3—Southern Morocco	As above
Area 4—Northern Morocco	As above
Area 5—Portugal	IPIMAR egg surveys October, November, January and March: 1185, 0186, 0386, 0388, 1090, 1091, 0397, 0199, 1199, 0300, 0102
Area 6—Northern Spain	IEO egg surveys March, April and May: 0388, 0490, 0591, 0492, 0592, 0395, 0595, 0397, 0399, 0400, 0500, 0301, 0401, 0302, 0303
Area 7—Eastern Biscay	AZTI egg surveys May/June 1999–2002
Area 8—English Channel	MBA time-series Station L5 Monthly means, all year 1947–1987

Table 2. *Spawning temperature parameters by area (see Table 1 for data sources).*

	Mean (°C)	Optimum (50% range,°C)	Overall (95% range,°C)
Areas 1 to 4—North-west Africa	—	16.00–18.00	15.50–20.00
Area 5—Portugal	15.59	14.55–16.35	13.35–17.10
Area 6—Northern Spain	13.99	13.15–14.35	12.40–16.75
Area 7—Eastern Biscay	15.73	14.70–16.50	14.20–18.50
Area 8—English Channel	13.76	13.00–14.70	9.90–17.85

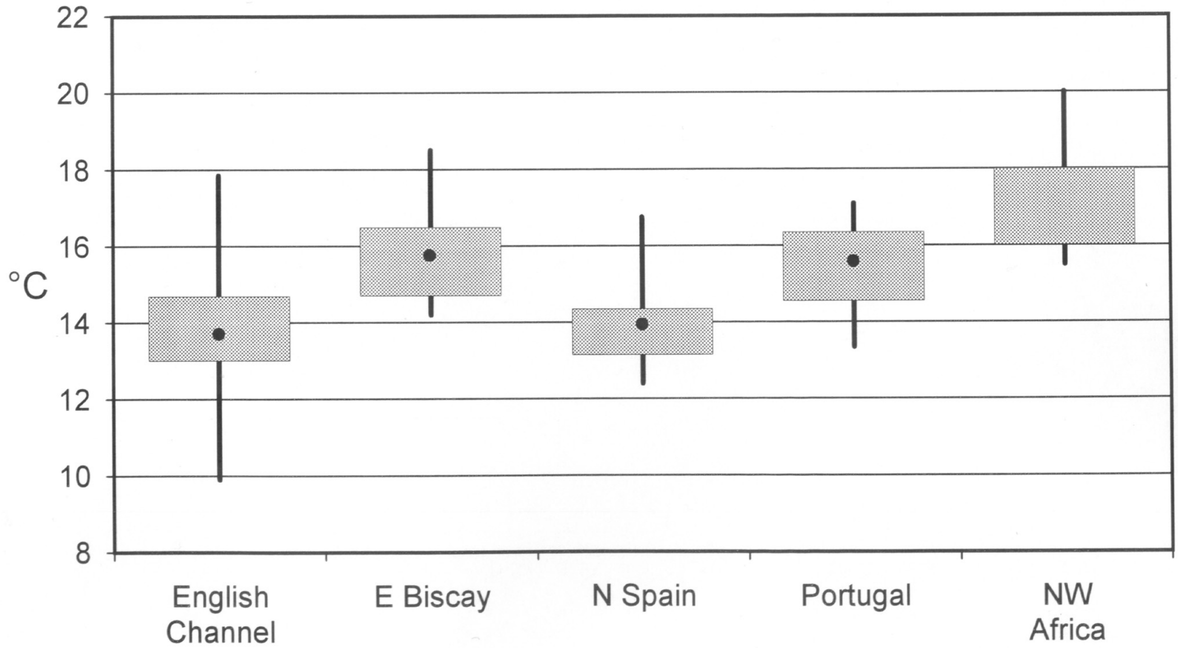

Figure 2. Spawning temperature parameters by area (see Table 1 for data sources). The black dots indicate mean spawning temperatures and the shaded boxes and vertical lines the optimum (50%) and overall (95%) spawning temperature ranges, respectively.

intervening area of northern Morocco and the Bay of Cadiz, the temperature range is slightly increased ($\Delta T \sim 6°C$) due to rather weaker summer upwelling. Off western Sahara, upwelling occurs throughout the year, which reduces the overall seasonal variation ($\Delta T \sim 4°C$). A relatively stronger seasonal signal ($\Delta T > 7°C$) reappears at the most southerly area, off Mauritania and Senegal, where upwelling occurs in the winter only, hence reducing temperatures at that time but not in the summer, resulting in an increased overall seasonal temperature range.

Comparison with the seasonal patterns of chlorophyll-*a* (Figure 3B) shows high chlorophyll concentrations (5–10 mg m^{-3}) in the southern areas of intense upwelling from southern Morocco to Mauritania and Senegal. The summer chlorophyll peak off southern Morocco and western Sahara corresponds to summer and all-year round upwelling, respectively, coupled with higher summer temperatures. The winter peak of chlorophyll off Mauritania and Senegal is related to the winter upwelling season. Slightly elevated chlorophyll levels are seen off Portugal where there is only relatively weak upwelling. At the northern end of the spawning distribution, in Biscay and the English Channel, chlorophyll levels were consistently low, particularly off the coast of northern Spain, with little seasonal signal (recognizing that the SeaWiFS chlorophyll data are from the surface layer only, and will not record sub-surface concentrations).

Based on coincidence of the annual temperature cycles and the optimum and overall spawning temperature ranges (Figure 3A), the predicted spawning seasons (Figure 4) are: English Channel (Area 8)—summer through autumn from May to November with summer and autumn peaks; eastern Biscay and northern Spain (Areas 6 and 7)—two clear seasons in spring/early summer from April to June, and late autumn (October–December); Portugal (Area 5)—a single extended season in winter/spring/early summer from October to May/June; northern Morocco (Area 4)—two seasons, in late autumn/early winter (September–December) and late spring/summer (March–July), with a notable gap in favourable temperatures in late winter (in part, a possible artefact from the shift in the derived generalized temperature ranges between Areas 4 and 5); southern Morocco (Area 3) and the western Sahara (Area 2) both have favourable conditions for much of the year outside the

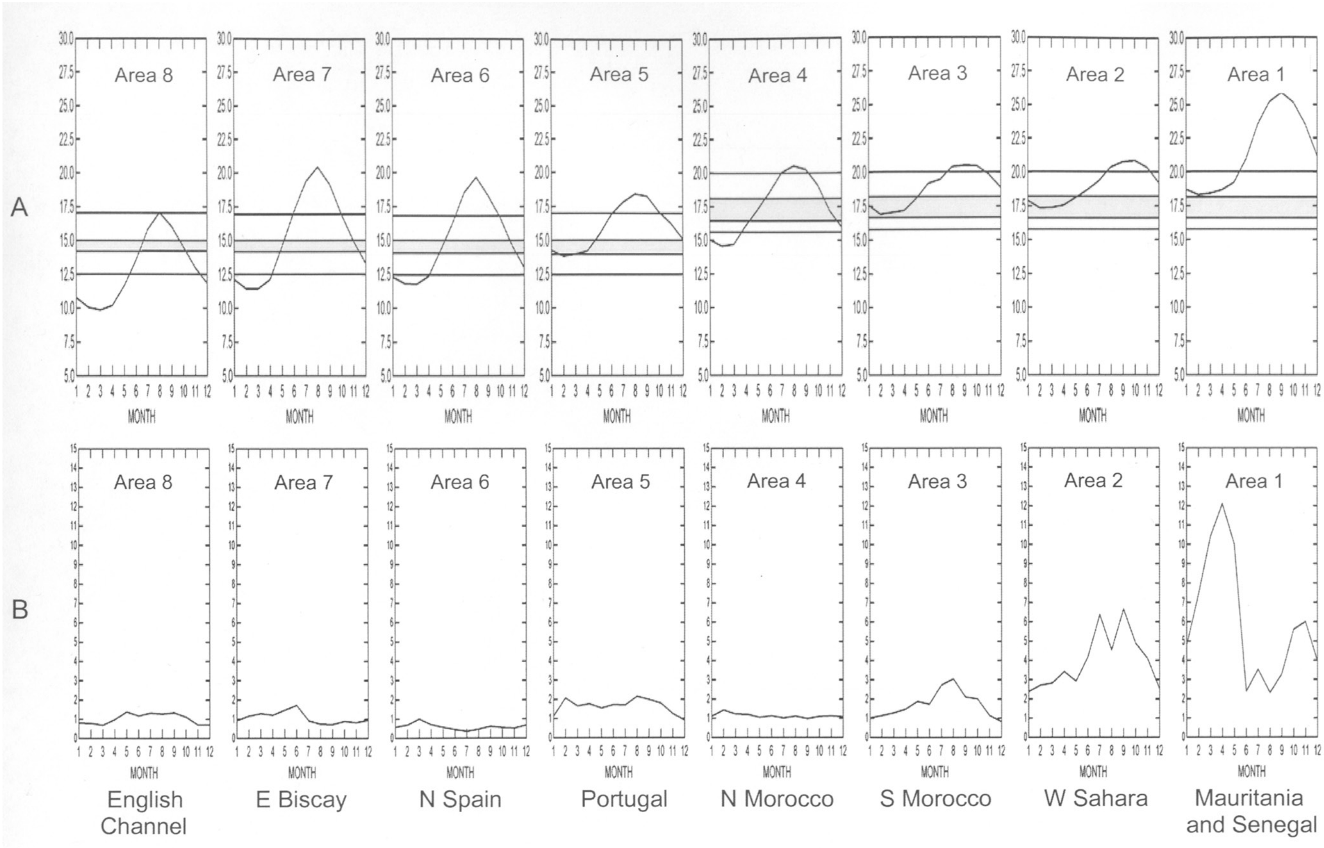

Figure 3. (A) Monthly mean SST variation (5–30°C, 1986–2002) for the eight areas along the mid-shelf line shown in Figure 1; the horizontal shaded bars represent the optimum spawning temperature range and the horizontal lines the overall range (see text); (B) monthly mean chlorophyll-*a* variation (0–15 mg m^{-3}, 1997–2002) along the same mid-shelf line.

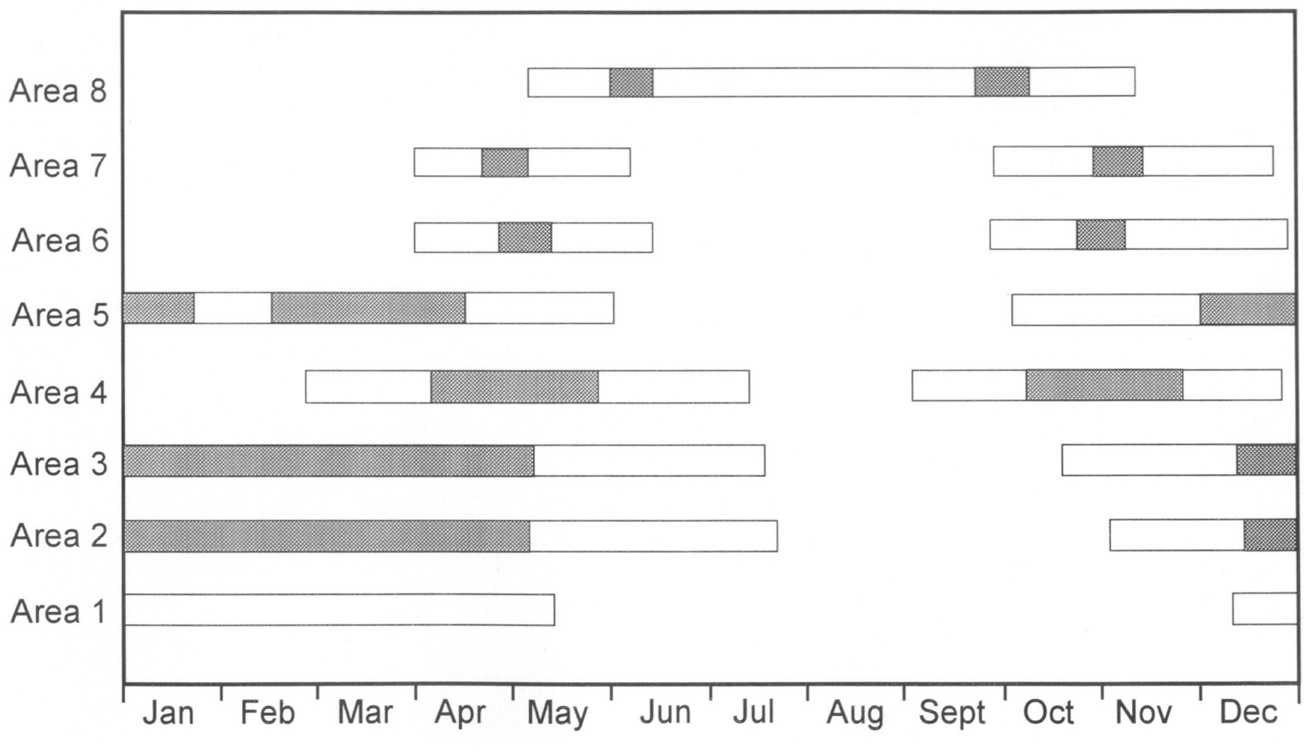

Figure 4. Seasonal extent of optimum (50% range—shaded areas) and overall (95% range—open areas) spawning temperatures, derived from Figure 3A for the eight areas along the mid-shelf line shown in Figure 1.

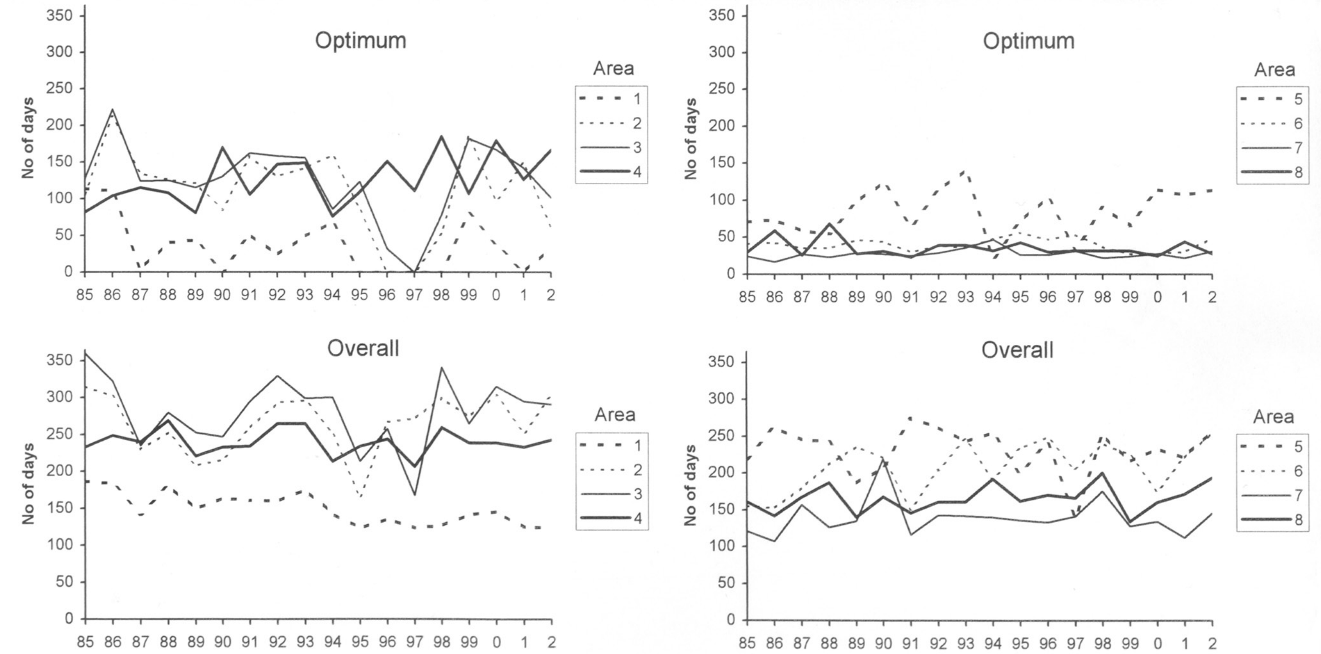

Figure 5. Annual variation by area (see Figure 1) in the numbers of days which fell within the optimum or overall temperature ranges for spawning.

Table 3. *Correlations between areas (see Figure 1) over the period 1985–2002 for the annual number of days in (A) the optimum spawning temperature range and (B) the overall spawning temperature range. Values significant at 5% are indicted by asterisks.*

A. Optimum temperature range.

	Area 1	Area 2	Area 3	Area 4	Area 5	Area 6	Area 7
Area 2	0.62*						
Area 3	0.54*	0.85*					
Area 4	−0.51	−0.44	−0.06				
Area 5	−0.22	−0.11	0.27	0.70*			
Area 6	−0.19	−0.50	−0.57	−0.18	−0.20		
Area 7	−0.03	−0.08	−0.34	−0.13	−0.15	0.31	
Area 8	0.17	0.32	0.29	−0.18	−0.11	0.02	−0.34

B. Overall temperature range.

	Area 1	Area 2	Area 3	Area 4	Area 5	Area 6	Area 7
Area 2	0.28						
Area 3	0.46*	0.66*					
Area 4	0.39	0.36	0.49*				
Area 5	0.30	0.38	0.69*	0.60*			
Area 6	−0.50	−0.23	−0.29	0.18	−0.21		
Area 7	−0.15	−0.23	−0.21	0.02	−0.14	0.35	
Area 8	−0.31	0.11	0.13	0.17	0.22	0.34	0.37

period of highest temperatures in late summer/autumn (August–October), with most favourable conditions occurring in winter/spring (January–May); in the most southerly area, Mauritania and Senegal (Area 1), temperature falls to within the overall range in winter/spring (December–May) but remains above the optimum range.

Interannual variation in extent of spawning temperatures

The inter-annual variability in number of days that temperatures fell within the optimum or overall spawning ranges is shown in Figure 5.

Western Sahara (Area 2), and southern and northern Morocco (Areas 3 and 4) had the longest extents of both optimum and overall temperature ranges (typically, 120 and 270 days, respectively), with markedly lower durations for both ranges in the most southerly area of Mauritania and Senegal (Area 1). A declining trend in the number of days in the overall spawning temperature range is observed for Mauritania and Senegal. The three most northerly areas, northern Spain (Area 6), eastern Biscay (Area 7) and the English Channel (Area 8), all had consistently low durations of optimum spawning temperatures (typically 30 days), with longer and more variable extents of the overall temperature range (Figure 5). The area off Portugal (Area 5) had an intermediate duration of optimum and overall temperatures, between values for the north-west African and the more northern areas.

Correlations of annual extents of optimum and overall spawning temperature ranges (Table 3) indicate a coherence from Portugal to Senegal (i.e. Areas 1 to 5).

DISCUSSION

Spawning seasons

The predictions of spawning seasons based on average annual temperature cycles are generally consistent with field observations, although with some differences: for example, in the English Channel, field sampling shows a marked reduction in egg abundance in August and September (Coombs et al., 2005), which is less evident in the temperature-based predictions; in Biscay, a definite autumn season from October to December is predicted from the temperature data, while only rather low and sporadic autumn spawning has been reported for this area (e.g. Solá et al., 1990); finally, for the north-west African regions, the predicted spawning seasons imply a rather more coherent pattern than occurs in reality, due to spatial and temporal variability in upwelling and topographic influences of coastal capes and bays on the current system (Binet, 1988; Ettahiri et al., 2003).

Part of the difference between predictions and observations may be due to bias in the parameterizations of spawning temperatures: in some areas data were available from year-round sampling at a single station, whereas in others there was wide geographical coverage, but restricted in seasonal extent (see comments in Results section); off north-west Africa there was a particular shortage of extensive field data. Additional factors include the potential bias in characterizing spawning temperatures using data along the mid-shelf line and the influence of the selected area boundaries. The possibility of different 'races', with different temperature adaptations, spawning at different times of the year is also a consideration, although genetics studies within the SARDYN project have indicated mostly a general cline in genetic characteristics with distance, rather than discrete populations; based on these genetics results, the most evident population break was in northern Morocco (Area 4), which is reasonably consistent with the inferred separation of European and north-west African areas on the basis of preferred spawning temperatures.

Otherwise, differences between the temperature-based spawning predictions and field observations may be related, in part, to variations in seasonal plankton production, on the basis that food availability can influence both spawning incidence of the adults (Peebles et al., 1996) and survival of the young stages (Heath, 1992). For the English Channel, the reduction in observed summer spawning, when temperatures are within the spawning range, can be associated with the dip in zooplankton abundance between the spring and autumn peaks (although this is not an invariable feature, see plankton time-series for the western English Channel—http://www.pml.ac.uk/L4). Conversely, in eastern Biscay the relatively low level of observed autumn spawning relates to the single plankton production season from March to July (e.g. Valdés & Moral, 1998).

However, sardine spawning is clearly not closely tied to plankton production and can have a variable relationship from area to area. From Biscay northwards, the seasonal occurrence of suitable spawning temperatures tends to coincide with increased seasonal plankton production. In the central regions off Portugal and Morocco, the winter months of suitable spawning temperatures, when there is maximum water column stability and minimum offshore transport, are outside the main plankton production period. At the southern end of the distribution, off western Sahara, Mauritania and Senegal, spawning is forced to times of upwelling to provide sufficiently low temperatures, but with coincident high production.

Inter-annual changes

The strong links in year-to-year spawning temperatures from Portugal to Senegal reflect a common oceanographic situation in the Canaries current/upwelling dominated system. Around Biscay, there is a weaker grouping of areas associated with a southern gyre of the North Atlantic Current (Pingree, 1993) and less dominant physical forcing.

Comparisons of predicted annual spawning success against observed stock indices are complicated by unknown links between spawning stock size, egg production and subsequent survival and year-class strength. This may account for the lack of any close agreement in the present study between annual variations in spawning temperature extents and observed field abundance of eggs from time series sampling in the English Channel (Southward et al., 2005) or from egg surveys in Biscay and western Iberia (ICES, 2005 and preceding reports).

Trends in the annual time-series of spawning temperature extent, which are essentially reflections of oceanographic conditions, are perhaps more likely to be reflected in fisheries/egg sampling data than individual annual variations. This is evident off northern Morocco where a declining trend in wind speed and upwelling through the 1970s and 1980s (Kifani & Gohin, 1992) has favoured increased winter spawning, which is consistent with the increasing trend in extent of optimum spawning temperatures for that area. However, a conflicting relationship is observed for the most southerly area of Mauritania and Senegal, which is generally beyond the southern limit of sardine spawning. This region has become increasingly favoured for spawning due to intensification of the trade winds and consequent upwelling of cool water through the 1970s and intermittently to 2003 (John et al., 1980; Binet, 1988; FAO, 2003), although a converse declining trend is seen in the present study in the number of days of spawning temperatures in the overall range. The lack of any consistent relationship is reinforced by observations of declining trends in spawning in Biscay and off Portugal through the 1990s (Stratoudakis et al., 2003), but with no equivalent trends in the present analysis of the annual extent of optimum or overall spawning temperatures.

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Appendix. *Spawning conditions and temperatures off north-west Africa.*

Regular sardine spawning occurs off north-west Africa, from the Strait of Gibraltar through Morocco and western Sahara as far as Cap Blanc (~21°N). South of this, off Mauritania and Senegal, spawning is relatively infrequent, depending on periods of cooling related to increased northerly wind stress and upwelling (e.g. John et al., 1980; Binet et al., 1998).

Seasonal changes in the trade wind affects the entire coastline from Senegal to north-west Spain, causing seasonal upwelling, mainly in the spring/summer in the north, and in the winter in the south; relatively continuous upwelling occurs all year round in the central region off northern Mauritania and western Sahara (e.g. Wooster et al., 1976). Upwelling conditions introduce cooler water which can be either favourable (for example, off Senegal where temperatures are lowered to within the preferred range for spawning) or unfavourable (for example, in spring off Morocco where upwelled water reduces temperature below the preferred range).

Off Morocco and the northern half of western Sahara, the main spawning season is in the winter (November–March; Furnestin, 1955; Sedletskaya, 1973; Roy et al., 1989) thus avoiding the most intense (April–October) upwelling period (Binet, 1988). Furnestin & Furnestin (1959) summarized seven years' data off Morocco showing this variability, with the main spawning season being in the winter and, to a lesser extent, in the spring.

Off the southern half of western Sahara and northern Mauritania, upwelling occurs all year round. Some spawning takes place in April/May but is more intense in October–December after the main upwelling period (Wooster et al., 1976; Roy et al., 1989). However, spawning periods and location may vary from year to year depending on environmental conditions (Ettahiri et al., 2003).

Off southern Mauritania the main peak of spawning is in January/February, within the extended period of winter/spring upwelling (November–June).

The duration of the upwelling season decreases from six months off northern Senegal (November to May) to one month off southern Senegal (January). The presence of some ripe female sardines caught in January–March off Senegal (Binet et al., 1998), indicates that spawning does occasionally occur this far south, and at least in the spring.

Typical spawning temperatures are in the range 15–18°C, and occasionally as high as 20°C (see below). This range is above the lower end of spawning temperatures recorded in Biscay and further northwards, where eggs are commonly found at temperatures <14°C. Furnestin & Furnestin (1959, 1970) suggest that, off Morocco, spawning is weak in cold winters (<16°C) and plentiful in warm winters (16–17.6°C).

Recorded spawning temperatures off north-west Africa

14–20°C	Furnestin, 1950
14.5–18.7°C	Furnestin, 1955
15.5–17.1°C	Binet, 1988
15.5–18°C	Binet et al., 1998
15.5–18°C	In winter, Ettahiri et al., 2003
17.5–21°C	In summer, Ettahiri et al., 2003
>16.5°C	Blackburn & Nellen, 1976
16.9°C	Maigret, 1974
16–18°C	Kifani & Gohin, 1992
17–18°C	Cruzado, 1974 (cited in Rubiés & Palomera, 1977)
15.5–20°C	Optimum at 16–18°C, Furnestin & Furnestin, 1970
15.8–17.4°C	Some up to 19.2°C, no eggs at <15°C, Sedletskaya, 1973
16–19.5°C	Maximum at 17.4–18.8°C, Ettahiri, 1996 (cited in Ettahiri et al., 2003)